A NEW PLOURDOSTEID ARTHRODIRE FROM THE UPPER DEVONIAN GOGO FORMATION OF WESTERN AUSTRALIA

by JOHN A. LONG

ABSTRACT. A new plourdosteid arthrodire, *Mcnamaraspis kaprios* gen. et sp. nov., is described from the Late Devonian (Frasnian) Gogo Formation of Western Australia. *Mcnamaraspis* is characterized by its very short spinal plate, larger pectoral fenestra and inferognathal with several distinct trenchant cusps. The anterior surface of the nasal capsule is covered by a hemispherical bone not previously recorded in placoderms. This is interpreted as an ossified annular cartilage, and, together with the interpretation of the suborbitalis muscle being present in arthrodires, supports the hypothesis that placoderms are more closely related to chondrichthyans than to osteichthyans. *Mcnamaraspis* is placed as the sister taxon to *Torosteus* in the family Plourdosteidae. The Plourdosteidae is redefined. Interrelationships of plourdosteids and relationships to other eubrachythoracid arthrodires are discussed.

THE superb three-dimensional preservation of the Gogo fishes is now well documented as many of the placoderms and osteichthyans from the fauna have been formally described (Miles 1971, 1977; Miles and Young 1977; Miles and Dennis 1979; Dennis and Miles 1979a, b, 1980, 1981, 1982; Dennis-Bryan and Miles 1983; Dennis-Bryan 1987; Long 1988a, b, c, 1990, 1994; Gardiner and Miles 1990). New seasons of field work at Gogo from 1986 to 1992 have yielded many new species, including the arthrodire described in this paper. As the bones are uncrushed and the armour of the placoderms can be accurately reconstructed, descriptions of new material can be kept concise by leaving the photographs, tables and illustrations to show main morphological features and proportions. The new arthrodire described herein is essentially similar to *Torosteus* (Gardiner and Miles 1990) in its general anatomy, so only different features or new anatomical data are here described in detail.

The plourdosteid arthrodires were a widespread group during the Late Devonian, being found in Canada (*Plourdosteus*; Vezina 1986, 1990), Russia (*Janiosteus*; Ivanov 1988), China (*Panxiosteus*; Wang 1991) and Australia (*Harrytoombsia*; Miles and Dennis 1979; *Kimberleyichthys*; Dennis-Bryan and Miles 1983; *Torosteus*; Gardiner and Miles 1990). They appear to have displaced the earlier coccosteid arthrodires that are commonly found in Middle Devonian faunas, particularly in the Old Red Continent of Euramerica (Denison 1978, 1984; Dineley and Loeffler 1993).

The hypothetical presence of annular cartilages in placoderms was one of several characters used by Stensiö (1963) to argue for a close relationship between placoderms and chondrichthyans, despite the absence of any fossil evidence. The new form described here shows, for the first time, the presence of ossified annular cartilages in a placoderm. Comparisons are made with the nasal structures of extant fishes and its bearing on placoderm affinities is discussed. In addition, aspects of the soft anatomy of the head are reconstructed from the structures preserved on the visceral surface of the skull roof and cheek.

Throughout the work the words 'length', 'breadth' and 'height' are abbreviated to as 'L', 'B' and 'H' respectively. Indices are expressed as ratios multiplied by 100. Institutional abbreviations are: BMNH, Natural History Museum, London, UK; WAM, Western Australian Museum, Perth, Australia.

SYSTEMATIC PALAEONTOLOGY

Class PLACODERMI McCoy, 1848
Order ARTHRODIRA Woodward, 1891
Infraorder BRACHYTHORACI Gross, 1932
Family PLOURDOSTEIDAE Vezina, 1990

1990 Torosteidae, Gardiner and Miles, p. 162.

Diagnosis. Eubrachythoracid arthrodires with moderately broad heads that lack both internasal and extrascapular plates; the postorbital plates and paranuchal plates are in extensive contact; the visceral surface of the skull-roof has well-developed, prominent postocular processes, and the lateral consolidated area has well-defined, triangular depressions; cheek unit loosely attached to skull-roof and submarginal plate free, well-defined spiracular notch present; parasphenoid with posterior depression immediately behind buccohypophysial foramen and with median hypophysial vein foramen present; trunk shield with a posterior lateral plate that deeply inserts into the ventral margin of the posterior dorsolateral plate; posterior ventrolateral plate has a prepectoral lamina contacting the anterior lateral plate.

Remarks. Vezina (1990) erected the family Plourdosteidae, to include *Plourdosteus*, *Panxiosteus*, *Harrytoombsia*, *Kimberleyichthys*, *Janiosteus* and *Eldenosteus*, based on fifteen characters, although few of these are unique to the referred taxa. Soon after Vezina's paper was published, Gardiner and Miles (1990) proposed the family Torosteidae, to include *Plourdosteus*, *Torosteus*, *Harrytoombsia* and *Kimberleyichthys*, based on fourteen characters, some of which were in agreement with Vezina's definition of the family Plourdosteidae, but again containing few unique characters within the subset of referred taxa. With the description of a new genus, obviously well-preserved, and exhibiting features of both familial diagnoses, it is here appropriate to redefine the family Plourdosteidae, and place Torosteidae in synonymy with this family. The characters used in the definition are all regarded as synapomorphies unique to the referred taxa (as known). In addition, the feature of the well-developed lateral consolidated area with triangular muscle attachment areas has been included, following on from comparisons made on the cheek anatomy of arthrodires in this paper. Other characters used by Vezina (1990) and Gardiner and Miles (1990) which characterize members of the group, but are not unique to the family Plourdosteidae, include: trilobate centrals; loss of internasal plate; skull roofing bones with sinuous suture lines and broad overlap areas; inferognathal plate with well-developed median cusps; postnasal plate large and seen in dorsal view; spinal plate may project laterally from trunk armour; posterior median ventral plate enlarged, being only a little longer than broad. The posterior lateral plate participates in the pectoral fenestra of one coccosteid, *Watsonosteus*, although this genus is regarded as one of the most specialized end members of that lineage and not related to the plourdosteids as it lacks all the defining skull characteristics of the latter group. The most characteristic feature of the posterior lateral plates of plourdosteids is that they possess a dorsal process that inserts deeply into a narrow cavity within the ventral margin of the posterior dorsolateral plate. This arrangement also occurs in

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EXPLANATION OF PLATE 1

Figs 1–8. *Mcnamaraspis kaprios* gen. et sp. nov. Holotype, WAM 86.9.676. 1, head shield in dorsal view, × 1·5; 2, headshield and cheek bones in left lateral view, × 1·5; 3, left inferognathal in mesial view, × 2; 4–5, right posterior superognathal in 4, mesial and 5, lateral views, × 3; 6–7, right anterior superognathal in 6, posterior and 7, anterior views, × 3; 8, right articular in lateral view, × 3. All specimens whitened with ammonium chloride.

PLATE 1

LONG, *Mcnamaraspis*
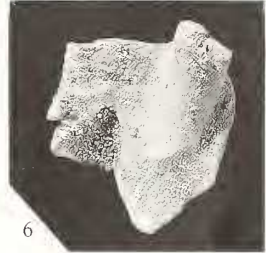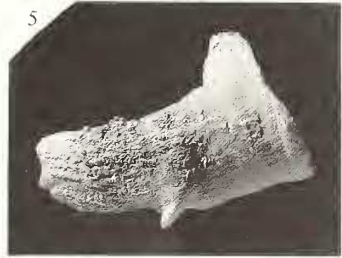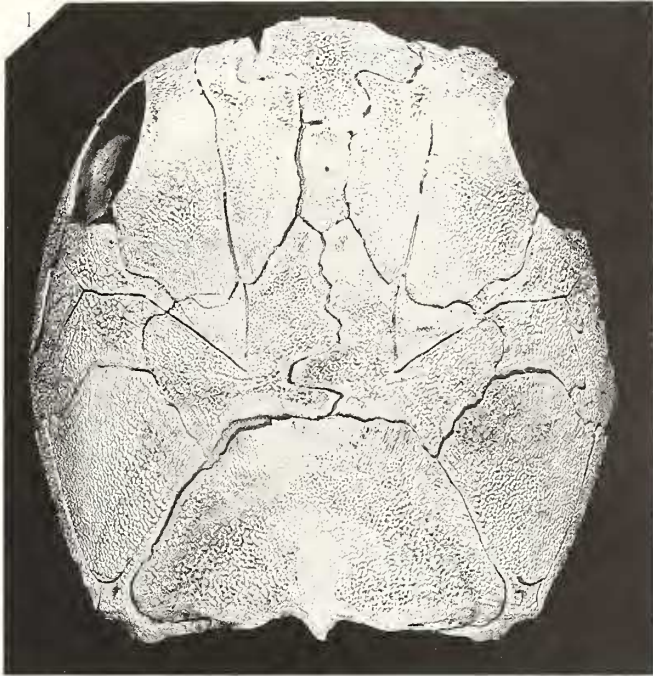
Eastmanosteus calliaspis (Dennis-Bryan 1987), but it appears to be a characteristic feature of all plourdosteids and is thus considered to have been acquired independently by *Eastmanosteus*, a dinichthyid (Long 1987). The genus *Eldenosteus* is currently being restudied by Heidi-Marie Johnstone and David Elliot at Northern Arizona University, based on new finds. It is excluded from comparison with other plourdosteids until descriptions of its anatomy are published.

Genus MCNAMARASPIS gen. nov.

Derivation of name. In honour of Dr Ken McNamara, Western Australian Museum, for his contributions to palaeontology.

Type species. Mcnamaraspis kaprios sp. nov., only known species.

Diagnosis. A plourdosteid arthrodire having a head shield slightly broader than long, with a nuchal plate thirty-nine per cent. of the skull length; inferognathals with two prominent anterior cusps; trunk shield with short spinal plate, nineteen per cent. as long as the median dorsal plate, and having greater contact with the interolateral plate than with the anterior ventrolateral plate; pectoral fenestra very large, being longer than the flank length of trunk shield.

Remarks. The unusually short spinal plate separates this genus readily from all other plourdosteids (Text-fig. 1).

Mcnamaraspis kaprios sp. nov.

Plate 1; Text-figures 1–14, 16–17

1988*a*   'a genus of plourdosteid arthrodire new to science', Long p. 442, fig. 6.
1990   *Torosteus pulchellus*, Gardiner and Miles pp. 175, 180.
1991   new genus of plourdosteid, Long, pp. 421, 425, pl. 4 C, D.

Derivation of name. Greek 'kaprios', like a boar, alluding to the well-developed lower jaw tusks on the inferognathal.

Holotype. WAM 86.9.676, an almost complete armour, including upper and lower gnathal elements, parasphenoid and partially ossified nasal capsules, wanting only the posterior ventrolateral plates and the left anterior ventrolateral plate (Text-figs 1–4, 6–14; Pl. 1).

Diagnosis. As for the genus.

Other material. BMNH P52553, a small skull and partial trunk shield, examined and measured by the author (Text-fig. 5).

Type locality. Bugle Gap (near locality 101 of Miles 1971), about 100 km east of Fitzroy Crossing, Western Australia. Gogo Formation (lower Frasnian). Collected by the author in August 1986.

Description

Head shield. The head shield (Pl. 1; Text-figs 2–5) closely resembles that of both *Harrytoombsia* (Miles and Dennis 1979) and *Torosteus* (Gardiner and Miles 1990), but differs principally in the shape of the nuchal plate (Nu) which is shorter in length, has a strongly indented posterior margin, and a weakly convex anterior margin. Skull roof bones generally have sinuous and irregular sutures and relatively broad overlap surfaces. The cheek unit is clearly visible on the skull in dorsal view (Text-fig. 3), and the orbital notches (orb) are also well defined. The nuchal plate on the holotype occupies only thirty-seven per cent. of the skull roof length (Text-fig. 4), and
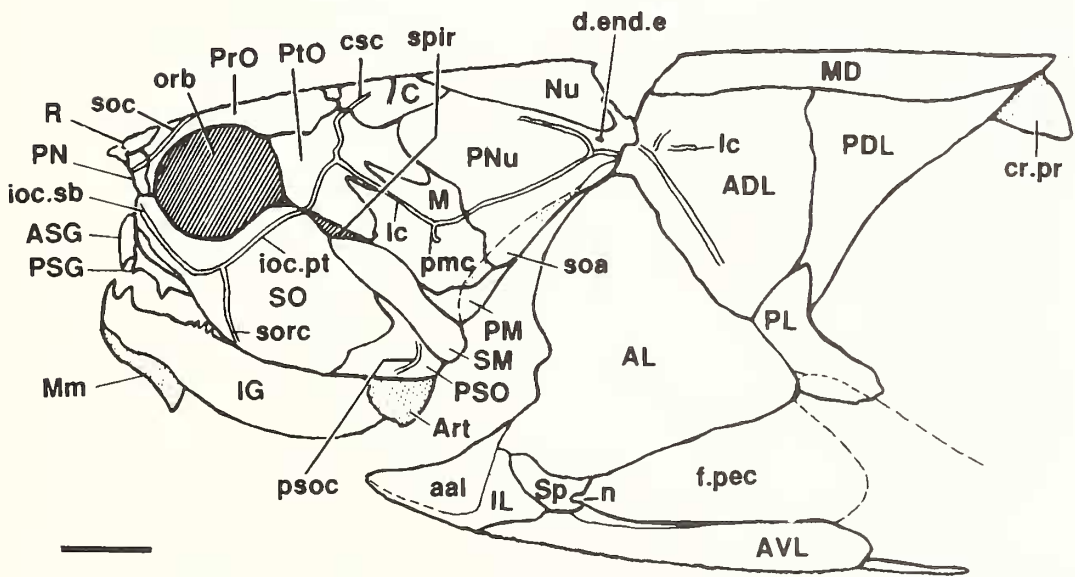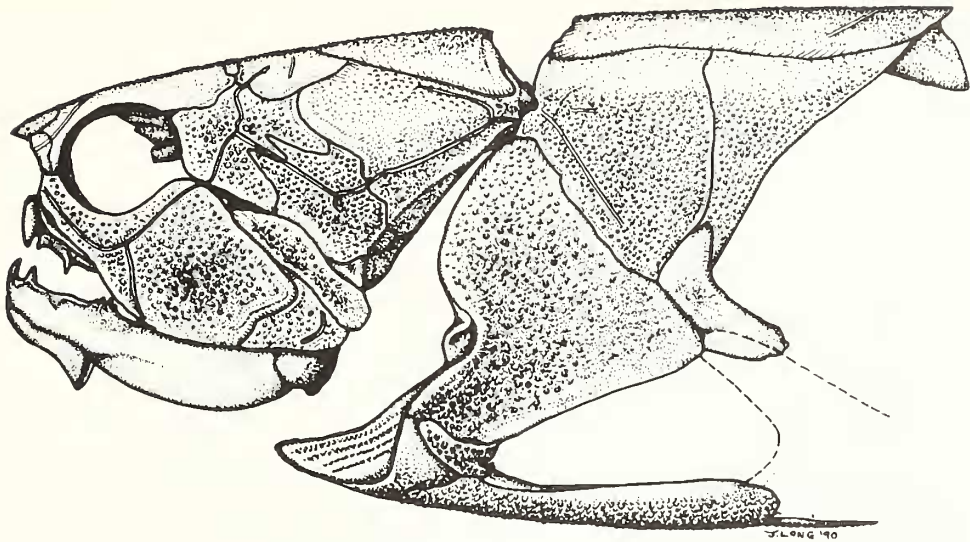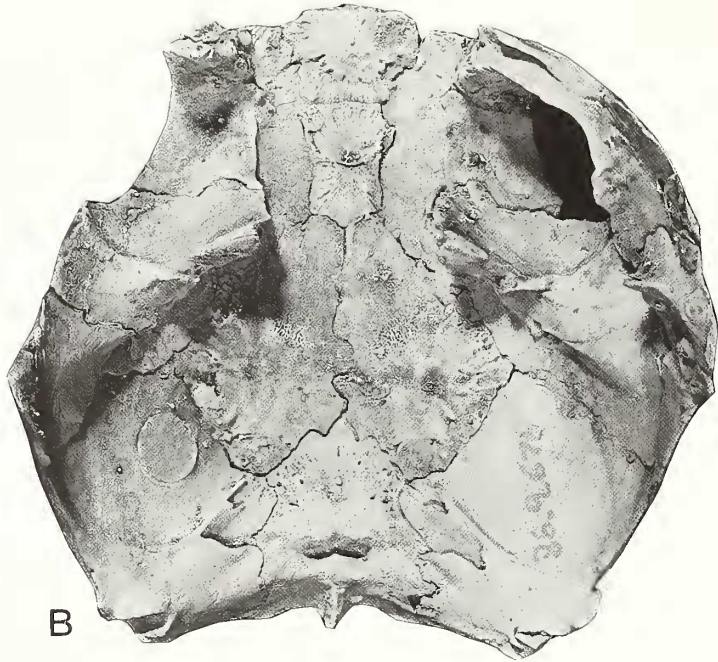
TEXT-FIG. 1. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. Armour in left lateral view. Scale bar represents 10 mm.

has a B/L index of 166 (for P52553 the nuchal is thirty-six per cent. of estimated skull length, B/L index of 162, Text-fig. 5). The nuchal has a weakly convex anterior margin, in contrast to the concave or indented anterior margins of all other plourdosteids. The paranuchal plate (PNu) has extensive contact with the postorbital (PtO), as in other plourdosteids, and the marginal plate (M) is strongly indented into the postorbital plate. The postorbital plate is significantly larger than the marginal. The postmarginal (PM) has a very small externally-ornamented area, most of the plate forming the posteriolaterally-facing subobstantic margin (soa). The pineal plate (P) is as long as the T-shaped squat rostral (R), the prepineal length of the skull
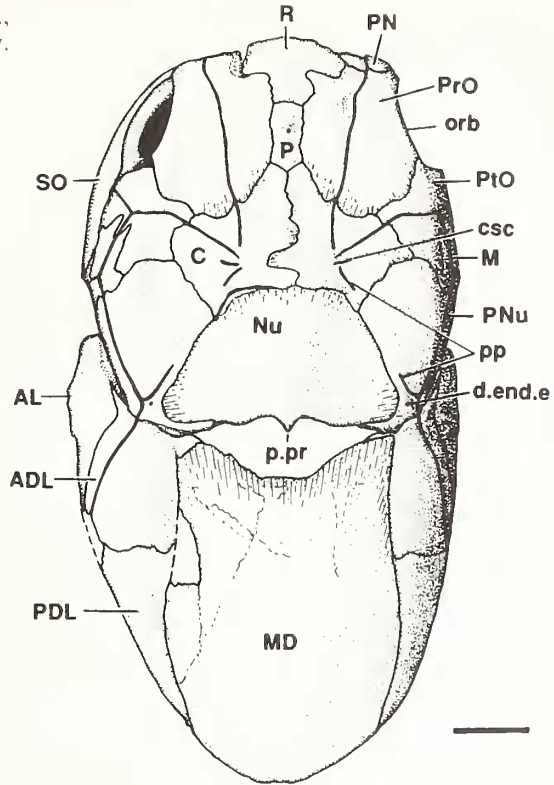
TEXT-FIG. 2. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. A, left side of cheek and skull roof in medial view, ×2; B, head shield and cheek bones in ventral view, ×1·5; both whitened with ammonium chloride.
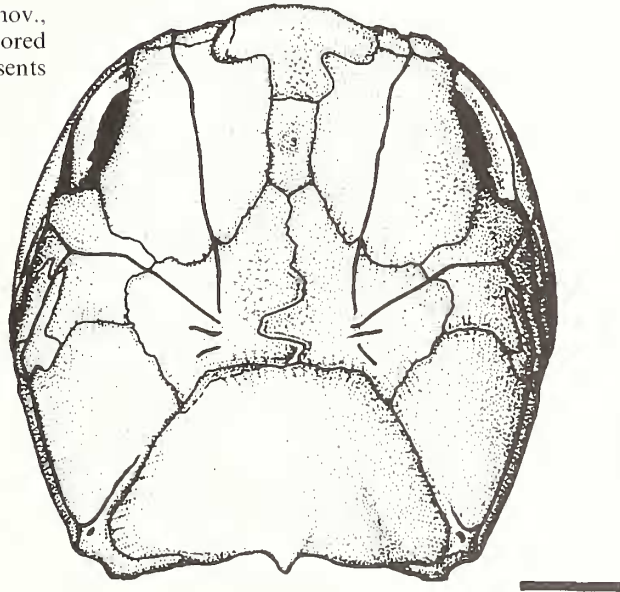
being twenty-five per cent. of the skull length. The postnasal plates (PN) both contact the rostral mesially and there are small accessory postnasal ossifications mesial to the postnasal bones in contact with the rostral (Text-fig. 6, acc. PN).

The visceral surface of the skull-roof shows all the regular morphological landmarks seen in eubrachythoracid arthrodires (Text-figs 2, 7). Of particular interest are the robust postocular processes (pt.o.pr) which have smaller, secondary processes here termed the 'hyoid processes' (pr.hy), developed

posterior to them. The width between the postorbital processes is 16 mm, narrower than for any other place where dermal bone encloses cartilaginous neurocranium. The triangular area posterolateral to these processes and bounded mesially by the lateral consolidated area (lcp) and anteriorly by a short ridge (ri, the

TEXT-FIG. 5. *Mcnamaraspis kaprios* gen. et sp. nov., BMNH P52553. Camera lucida sketch of head shield in dorsal view. Scale bar represents 5 mm.

TEXT-FIG. 6. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. Camera lucida sketch of left and right anterior margins of the head shield showing position of accessory postnasal bones. Scale bar represents 1 mm.

'postsuborbital crista' of Carr 1991, p. 381). It is a well-defined depression (tri) for muscle attachment coming from the dorsal region of the cheek unit, and is discussed further below.

The cheek plates (Pl. 1; Text-figs 1, 8), of both sides are well-preserved and resemble the pattern seen in *Torosteus* except for the narrower suborbital process on the suborbital plate (SO). The submarginal plate (SM) is elongate and contacts the marginal and postmarginal plates, leaving a spiracular notch (spir) between the postorbital plate and the dorsal margin of the suborbital plate. The anterior end of this notch is closed by short contact between the suborbital and postorbital plates, unlike the open spiracular notch in *Torosteus* and *Harrytoombsia*. The postsuborbital plate (PSO) has a well-developed subcutaneous pit and cuspate sensory-line groove (psoc), but the suborbital plate lacks the subcutaneous pit seen in other plourdosteids. The
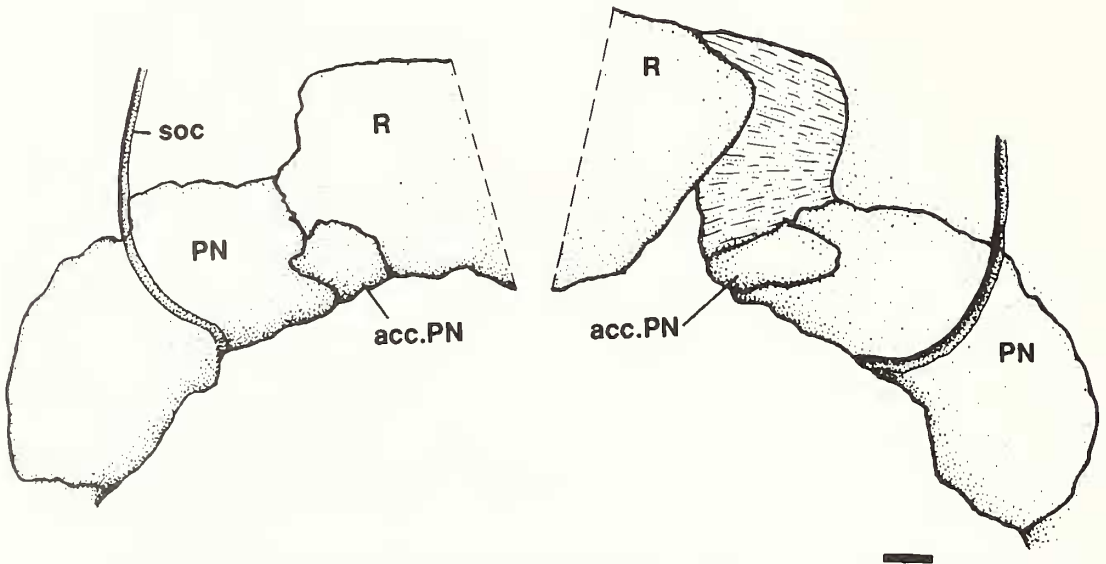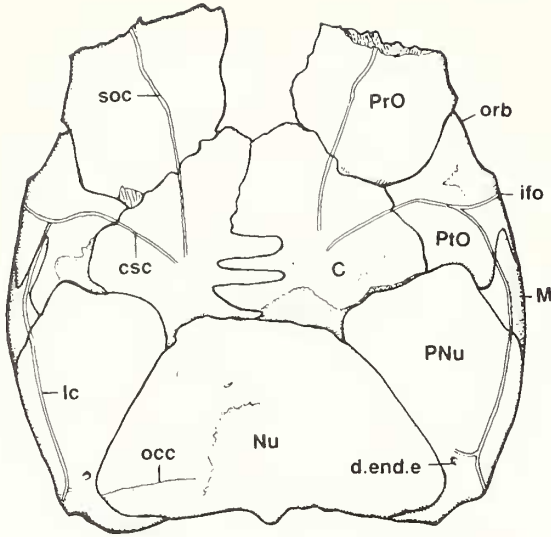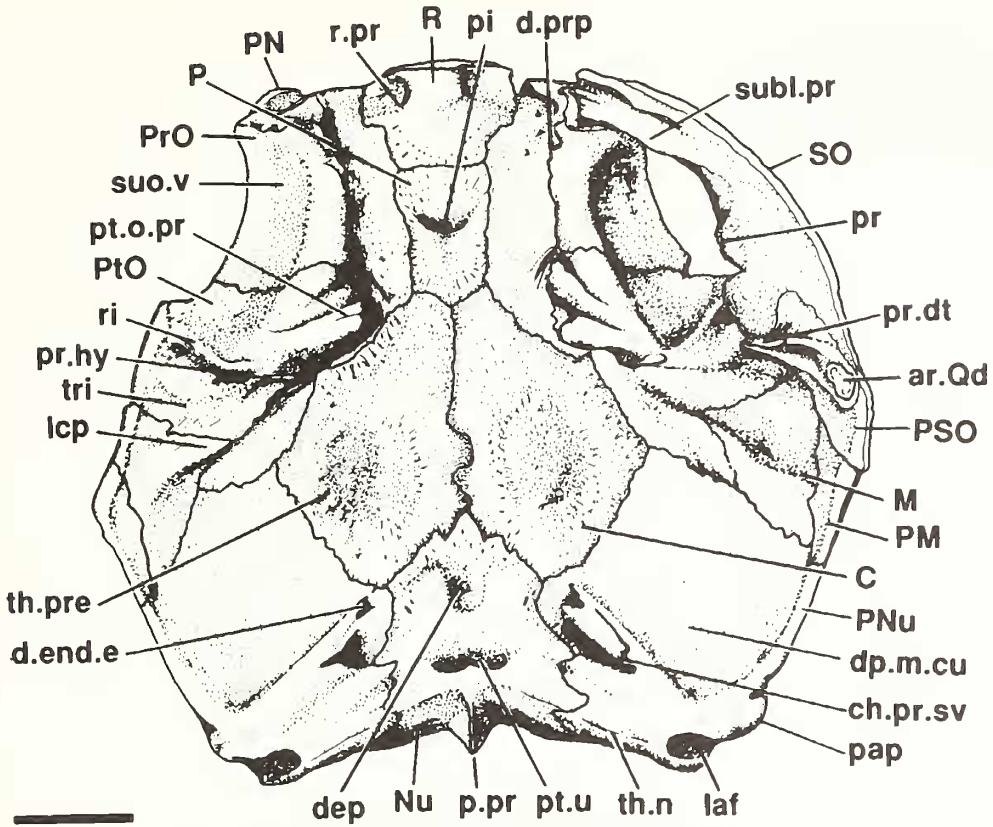
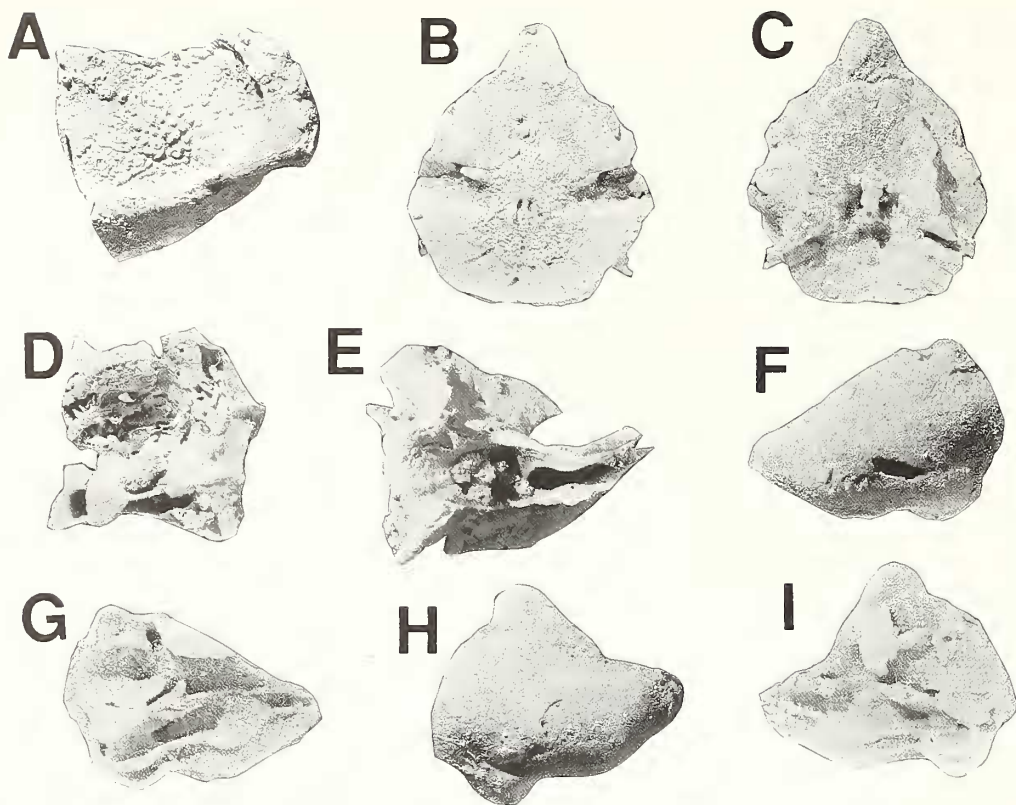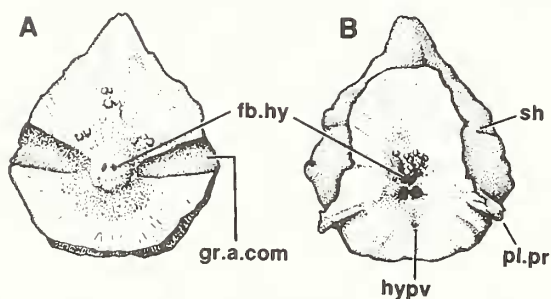TEXT-FIG. 7. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. Head shield and left cheek bones in ventral view. Scale bar represents 10 mm.
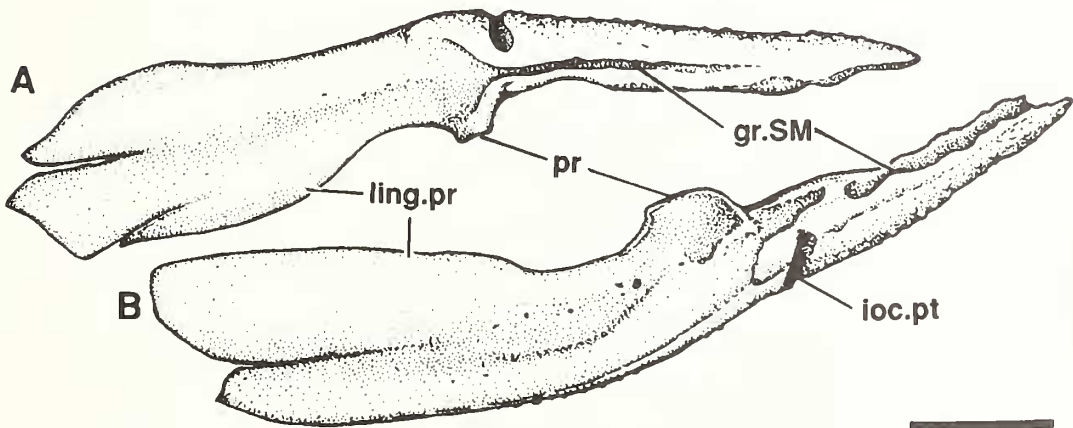
TEXT-FIG. 8. A, *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676; camera lucida sketch of right suborbital plate in dorsal view. B, *Torosteus tuberculatus*, holotype, WAM 40.4.262; left suborbital plate in dorsal view. Scale bar represents 5 mm.
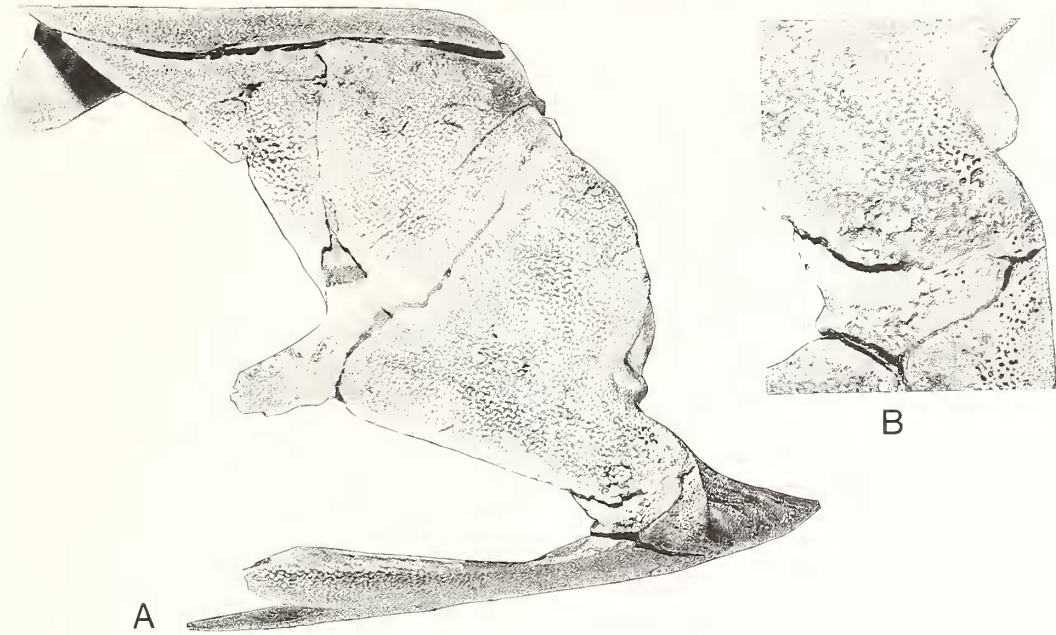
TEXT-FIG. 9. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. A, right articular in mesial view; B–C, parasphenoid in B, ventral view; and C, dorsal view; D–E, left side of ethmoid ossification in D, anterior view; and E, lateral view; F–I, annular cartilages from both sides of nasal capsules in F, H, anterior view; and G, I, posterior view. A–E are × 3; F–I × 4.

TEXT-FIG. 10. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. Camera lucida sketch of parasphenoid in A, ventral view; and B, dorsal view. Both × 2·73.

suborbital plate has a well-defined dermal process eminating from near the dorsal end of the orbital margin, along the mesial edge. This process (Text-figs 2, 7–8, pr) occurs in all other Gogo plourdosteids and is discussed more fully below.

The dentition is characteristic for the genus in that the inferognathal (Pl. 1, fig. 3; Text-fig. 1, IG) has three strong mesial 'teeth', two large anterior biting cusps, a trenchant crest with cutting edges on both labial and lingual edges, and well formed posterior teeth at the rear of the biting division of the inferognathal. The anterior superognathal (Pl. 1, figs 6–7; Text-fig. 1, ASG) has three biting cusps, a large trenchant median cusp and two sharp smaller cusps developed on the posteroventral corner of the biting margin. The posterior superognathal (Pl. 1, figs 4–5; Text-fig. 1, PSG) is remarkably thin compared with those of *Harrytoombsia*,

TEXT-FIG. 11. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. A, trunk shield in right lateral view, × 1·5; B, enlargement, showing right spinal plate, × 3.

Torosteus and *Kimberleyichthys*, and has a characteristic sharp cusp directed posteroventrally from its centre. The dorsal process of the posterior superognathal is well-developed, but the greatest width of the bone is still only 0·6 of its length, this being shorter than for the other Gogo plourdosteids.

The parasphenoid (Text-figs 9B, C; 10) has a pentagonal shape with a weakly convex posterior margin, although in all other respects it is not unlike that of *Torosteus pulchellus* (Gardiner and Miles 1990, fig. 24). The dorsal surface (Text-fig. 7B) has a well-defined rectangular rim separated from the ventral surface by an extensive prehypophysial shelf (sh). The central area is strongly depressed for the buccohypophysial foramina (fb.hy), with a robust median longitudinal crest separating them. Paired posterolateral processes (pl.pr) are developed. The opening for the median hypophysial vein (hypv) is well-defined.

No extrascapular plate was found in the specimen, and, as all other parts of the anterior of the skeleton were preserved, it is reasonable to assume that an extrascapular plate was lacking from the armour as in other plourdosteids.

The trunk shield (Text-figs 1, 3, 11–13) is missing only the posterior ventrolaterals and the left anterior ventrolateral plates. The presence of an enclosed pectoral fenestra (f. pec.) is demonstrated by the overlap area on the posterior lateral plate (PL) for the postpectoral lamina of the posterior ventrolateral plate. The pectoral fenestra was very large relative to the size of the lateral wall of the trunk shield, more so than for any other plourdosteid. The anterior lateral plate (AL) is characteristic for the genus within plourdosteids in having a nearly pointed dorsal margin, well-defined semicircular embayment for the overlap of the submarginal plate (the post branchial lamina), short spinal overlap margin, and an extensive, straight margin bordering the pectoral fenestra. The most diagnostic feature of the trunk shield is the very short spinal plate (Text-figs 1, 11B, 13, Sp) which is only twenty-one per cent. of the length of the medial dorsal plate, compared with thirty to thirty-six per cent. in *Torosteus* species. The spinal (Sp) has no posteriorly facing lamina as in *Torosteus*, and is embayed with a small posterior notch (n). The contact margin between the spinal and the interolateral (IL) is more than twice as long as the contact margin between the spinal and anterior ventrolateral plates (AVL).

The median dorsal (MD), anterior dorsolateral (ADL) and posterior dorsolateral (PDL) plates show no special features; their shapes are shown in Text-figures 1–3, 11 and 12. Their proportions are incorporated into the measurements for the trunk shield (Table 1). The posterior lateral (PL) plate is strongly bent, and is much narrower than for *Torosteus* or *Harrytoombsia*.

TEXT-FIG. 12. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676, anterior half of trunk shield in ventral view, × 1·5.
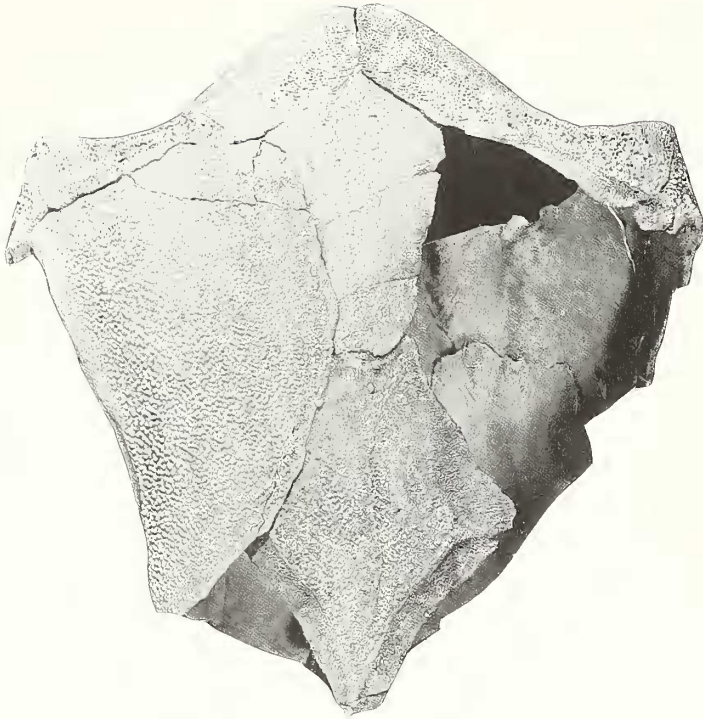
TEXT-FIG. 13. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. Anterior half of trunk shield in ventral view. Scale bar represents 10 mm.
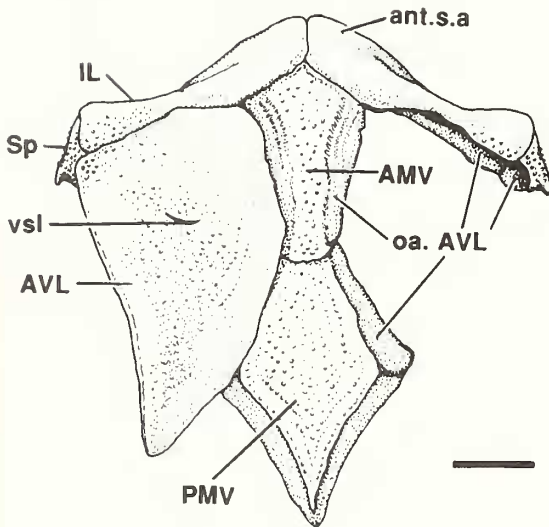
The anterior and posterior median ventral plates (Text-figs 11–13, AMV, PMV) are of similar length, the latter being about a third broader than the anterior median ventral plate. The interolateral plate is similar to that in other plourdosteids, such as *Torosteus* and *Harrytoombsia* and shows no special features apart from the well-defined anterior ventral shelf (Text-fig. 13, ant. s.a.).

TABLE 1. Measurements of *Mcnamaraspis kaprios* Holotype, WAM 86.9.676.

1. Skull roof length – 56·3 mm	13. Length of inferognathal – 38·5 mm
2. Breadth skull-roof – 57·7 mm	14. Length of biting division of inferognathal – 17·7 mm
3. Breadth of skull across posteromesial angles – 41·2 mm	15. Breadth of trunkshield – 64 mm
4. Depth of headshield – 35 mm	16. Depth of trunkshield – 63 mm
5. Prepineal length – 13·9 mm	17. Length of rostrocaudal flank of trunkshield – 26·5 mm
6. Length of orbit – 14 mm	18. Length of pectoral fenestra – c. 30 mm
7. Nuchal length – 20·9 mm	19. Median dorsal plate length – 43·8 mm
8. Length of lateral articular fossa – 5·3 mm	20. Median dorsal plate breadth – 35·2 mm
9. Depth of lateral articular fossa – 2·7 mm	21. Length of spinal – 9·4 mm
10. Angle between lateral articular fossa and headshield – 30°	22. Angle between spinal and midline of armour – 13°
11. Length of cheek – 40·5 mm	23. Anterior ventrolateral plate length – 44·8 mm
12. Length of postorbital division of cheek – 24·9 mm	24. Length of spinal division of anterior ventrolateral plate – 8·75 mm
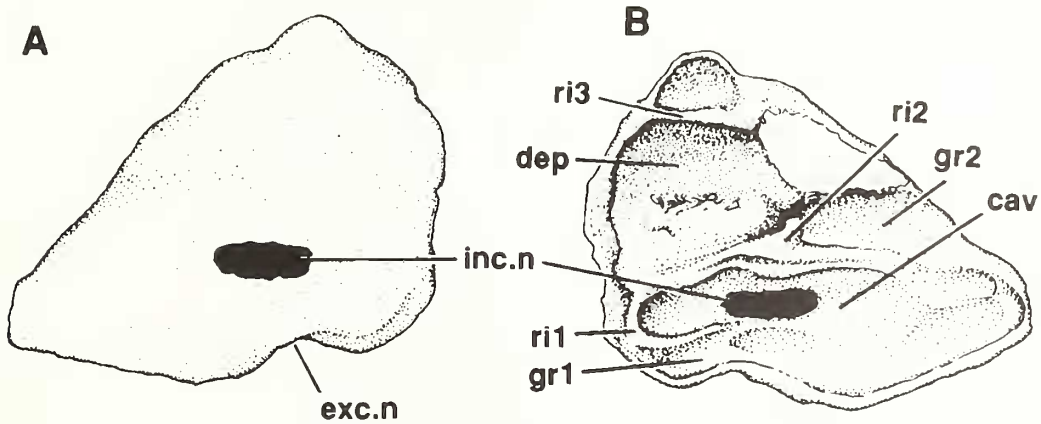
TEXT-FIG. 14. *Mcnamaraspis kaprios* gen. et sp. nov., holotype, WAM 86.9.676. Annular cartilage in A, anterior view; and B, posterior view. Scale bar represents 1 mm.

NEW ANATOMICAL FEATURES FOR ARTHRODIRES

The well-preserved holotype exhibits a number of features never described before in arthrodires or for placoderms in general, or which have only been alluded to in previous descriptions. These include: the first occurrence of annular cartilages; the development of muscle attachment areas for the opercular regions; the presence of bony processes on the suborbital plates; and the presence of additional postocular processes on the visceral surface of the skull roof.

Annular cartilages. The specimen shows preservation of two perichondrally ossified irregular hemispheres (Text-figs 9F–I; 14) which were attached to the front of the snout. As the anterior part of the ethmoid bone was preserved it is possible to fit one of these bones over the front of the cavity for the nasal capsule. The neat fit of the hemispherical bone over the nasal cavity, and the presence of a small slit-like opening for the naris in the bone, suggests that it was an ossified cover to the nasal capsule. In chondrichthyans, an annular cartilage rings the nasal cavity and covers the front of the

nasal capsule (Stensiö 1963). Although Stensiö preferred to restore the annular cartilage in the snouts of arthrodires, there was no fossil evidence for this bone being present in any of the placoderms that he studied. The new Gogo specimen provides the first evidence of an annular cartilage being developed in placoderms. Why only these genera show the feature is not known, but it does not preclude the possibility that it was present as unossified cartilage in other placoderms, and ossified in only a few cases, such as in *Mcnamaraspis*.

In its external shape, viewed anteriorly, the annular cartilage bone is lacriform (Text-fig. 14). The external surface is smooth and strongly convex with a small sloping slit, presumably for the incurrent naris (inc.n). The excurrent naris (exc.n) is represented by a notch in the ventral margin of the annular cartilage. This notch is well defined when the bone is fitted over the anterior face of the nasal capsule. The visceral surface (Text-fig. 14B) shows a large cavity around the incurrent naris (cav) and a series of depressions (dep), ridges (ri 1–3) and grooves (gr 1, 2), which in life may have braced a sinuous folded cartilage structure, much like the complex annular cartilage seen in many elasmobranchs (e.g. *Isurus punctatus*; Stensiö 1963, fig. 33). The function of this structure would have been to direct the flow of water from the incurrent naris around the olfactory organ, and out through the excurrent notch. In many sedentary elasmobranchs the annular cartilage is highly specialized, allowing for communication between the nasal openings and the mouth (Bell 1993), and therefore the primitive condition is seen in most free-swimming sharks. *Mcnamaraspis*, having been an active free-swimming predator, also exhibits a simple, unspecialized annular cartilage not too unlike that of modern pelagic sharks such as *Isurus*. As the annular cartilage of *Mcnamaraspis* did not develop nasoral grooves, the flow of water in and around the olfactory organs, situated anterior to the roseate cribrosal bone, was most likely functional purely in olfaction, without any likelihood of involving respiration. It has been suggested that some placoderms, like the antiarch *Bothriolepis*, had paired lung-like structures (Denison 1941) and thus it could be argued the nasal capsules and their surrounding soft tissues may have secondarily developed respiratory specializations, although this has not been alluded to in any descriptions of the rostral bones or preorbital recesses of that genus (e.g. Stensiö 1948; Young 1984).

Suborbital bone – orbital autopalatine process. The additional small process found on the inside orbital margin of the suborbital bone in *Mcnamaraspis* (pr, Text-figs 7–8) has also been identified by the author in several other Gogo plourdosteids (*Harrytoombsia*, *Torosteus pulchellus*, *T. tuberculatus*) but is absent from *Eastmanosteus*, *Incisoscutum*, all the camuropiscids and the two new, undescribed forms of Gogo 'coccosteomorph arthrodires' currently being studied by workers at the Natural History Museum, London. The process was termed the 'mesial process' by Gardiner and Miles (1990) who suggested that it 'was probably for a branch of the adductor mandibulae muscle'. The process emanates from near the top of the orbital margin of the suborbital plate in *Mcnamaraspis*, and in the middle of the orbital margin in *Torosteus*. The process is situated more ventrally than the dermal articular ridge on the mesial margin of the suborbital plate of *Buchanosteus* (Young 1979, p. 333) and did not take part in any connection with the skull roof. When the cheek unit and jaw cartilages are articulated to the skull roof it is clear that the process aligns well with the posterior margin of the ossified division of the autopalatine and would have most probably have served as a bracing point or attachment point for a lateral ligamentous connection from the autopalatine to the suborbital plate. This is well demonstrated in the holotype of *Torosteus pulchellus* (Gardiner and Miles 1990, fig. 20) where the process can be seen emanating from the suborbital plate lateral to the posterior margin of the autopalatine. The strap-like palatoquadrate would have passed directly lateral to the process, and thus it could not have served as an attachment point for adductor mandibulae muscles. These muscles are here reconstructed as in *Squalus* (Text-fig. 15) inserting dorsally on the ventral concave surface of the palatoquadrate (Text-fig. 16). Thus the small mesial process can be termed 'an orbital autopalatine process' of the suborbital bone. This character would appear to be a strong synapomorphy uniting these Gogo taxa, and possibly may characterize the whole plourdosteid group if it can be identified within the other non-Australian genera.

TEXT-FIG. 15. *Squalus acanthias*, outer muscles of the head and pharynx (after Gans and Parsons 1964).

spiracular slit

spiracular muscle

levator arcus palatini

levator hyoideus
cucullaris

adductor mandibulae

hyoideus constrictor dorsalis

superficial constrictor dorsalis
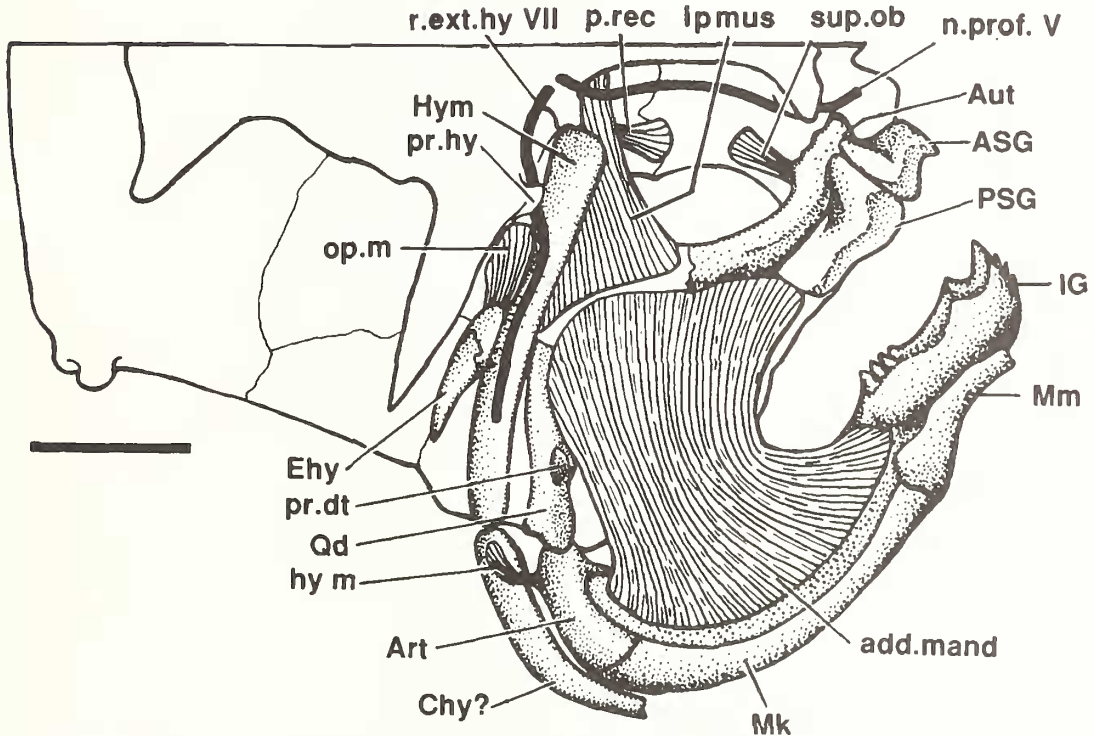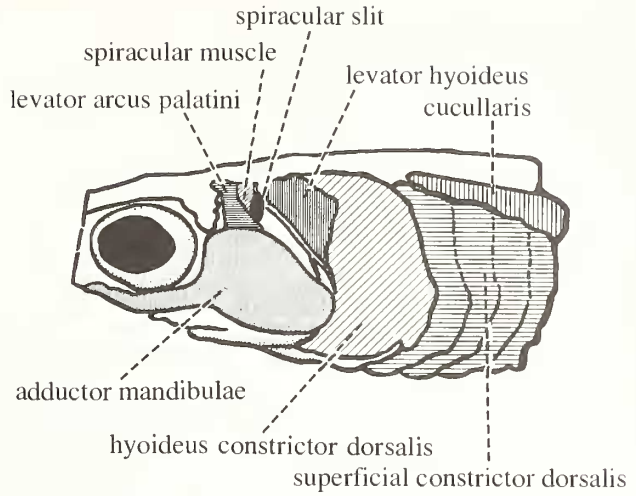
TEXT-FIG. 16. *Mcnamaraspis kaprios* gen. et sp. nov. Attempted reconstruction of soft anatomy of the cheek and jaw regions. Scale bar represents 10 mm.

Reconstructing jaw and opercular musculature. The lateral consolidated area of the skull roof is divided by a ridge (ri, Text-fig. 8) which separates the suborbital vault (suo.v) from a large triangular ventrally facing depression (tri). When the cheek unit is articulated with the skull roof this depression is adjacent to the postsuborbital plate, thus showing that it would have served as an attachment area for musculature that inserted on the visceral surface of the skull roof dorsal to the palatoquadrate. The adductor mandibulae muscles would have passed ventrally from the
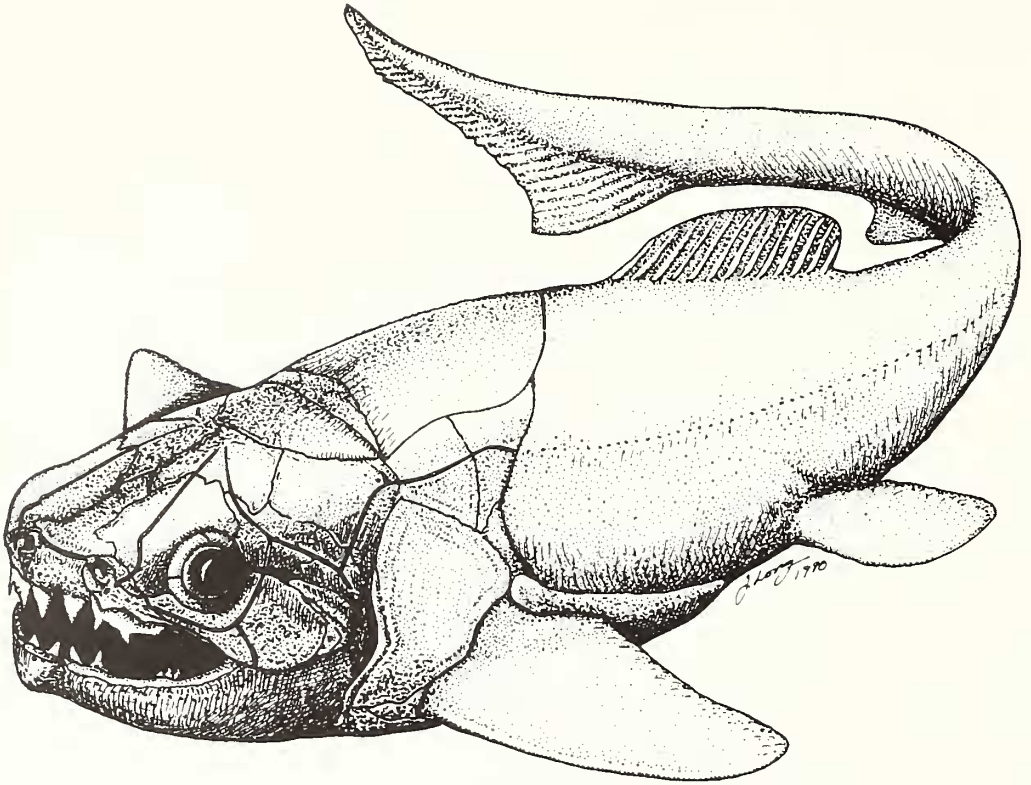
TEXT-FIG. 17. *Mcnamaraspis kaprios* gen. et sp. nov. Restoration of living fish, tail based on *Coccosteus cuspidatus* (Miles and Westoll 1968) and *Torosteus* (WAM 91.4.32).

palatoquadrate to insert along the mesial face of the inferognathal, as is normal of most fishes. Therefore I suggest that the triangular depression on the lateral consolidated area of the skull roof probably served as an attachment site for the levator palatoquadratini muscle (l.p. mus, Text-fig. 16), as occurs in this position in many osteichthyan and elasmobranch fishes (Text-fig. 15; Edgeworth 1935; Gans and Parsons 1964; Lauder and Liem 1983). This muscle would have facilitated movement of the cheek unit for respiration. Immediately posterior to the triangular depression is a smaller, less well-defined area where the lateral consolidated region tapers to the posterolateral corner of the skull roof. This weakly depressed area of dermal bone may have served as an attachment area for the smaller opercular muscle emanating from the perichondral ossification of the submarginal plate, here called an epihyal element. This ossification is only seen in one Gogo specimen, the holotype of *Torosteus pulchellus* (WAM 88.2.7) and may well be interpreted alternatively as an opercular cartilage as argued by Young (1986, p. 39). If so, the hyomandibular element, not perichondrally ossified in any Gogo arthrodire, would have to be reconstructed between the palatoquadrate and the epihyal/opercular cartilage element. For the purposes of reconstruction here the small ossification of the submarginal seems more likely to be an opercular cartilage, as it is situated adjacent to the weakly depressed area on the skull roof here interpreted as a suitable attachment site for the opercular muscle (Text-fig. 16). However, the true 'epihyal' element may well be situated posteroventral to the opercular cartilage as suggested by Young (1986).

With regard to the adductor mandibulae in arthrodires, the presence of a slender suborbital division of bone on the suborbital plate would suggest that the suborbitalis muscles were well-defined, extending forwards and possibly meeting in a midline raffe. These muscles, along with the

levator palatoquadratini, serve to protract and retract the palatoquadrate in chondrichthyans (Edgeworth 1935), and in arthrodires would have worked with the opercular muscle to move the cheek unit during respiration. Changes in water volume within the buccal cavity may have been regulated by these suggested lateral movements of the dermal cheek unit, forming a simple buccal pump mechanism. This degree of mobility of the cheek unit is not seen in many arthrodires, as several groups have the cheek fixed rigidly to the trunk shield (e.g. camuropiscids, brachydeirids, selenosteids, etc.). In these forms, and other placoderms lacking a separate cheek complex, expulsion of water from the gill chamber would have been achieved by vertical movements of the head shield working in conjunction with gill arch muscles to force water out the branchial opening behind the submarginal plate.

Postocular processes and hyoid process. The robust postocular processes of the plourdosteids are better developed than for any other arthrodire and most probably represent an adaptation for bracing or supporting the cartilaginous endocranium during the powerful bite. In addition to the robust anterior postocular process seen in *Mcnamaraspis*, there are a pair of smaller, delicate processes immediately posterior to the larger postocular processes. These smaller processes I have termed the 'hyoid processes' (pr.hy, Text-figs 7, 16) as they correspond well with the position of the ramus hyoideus nerve emerging from the anterior region of the posterior postorbital process of the braincase (as in *Buchanosteus*; Young 1979), and presumably continuing down to the hyomandibular. These hyoid processes are also observed in *Torosteus* and *Harrytoombsia*. Text-figure 16 shows an attempted reconstruction of some aspects of the soft anatomy of *Mcnamaraspis* based on the new morphological observations discussed above.

Text-figure 17 shows an attempted reconstruction of *Mcnamaraspis* as a living fish with the tail restored after *Coccostens cuspidatus* (Miles and Westoll 1968). The axial skeleton of the body from the trunk to the anal fin is preserved in one of the Gogo plourdosteids (*Torosteus* sp., WAM 91.4.32) showing these bones to be almost identical with those of *Coccosteus*.

PHYLOGENETIC IMPLICATIONS

Relationships of plourdosteids within the eubrachythoracids. The following discussion of arthrodire interrelationships deals only with the higher eubrachythoracids, defined as a monophyletic group by Lelievre *et al.* (1987), Carr (1991) and Lelievre (1991). The eubrachythoracid arthrodires are defined by having: (1) separate autopalatine and quadrate ossifications of the palatoquadrate; (2) development of a continuous thickening across the posterior margin of the head shield; and (3) the supraorbital vault developed as part of the lateral consolidated arch which is bounded posteriorly by a posterior supraorbital crista (Carr 1991). Lelievre (1991) also used the position of the orbits as lateral on the headshield and the development of a suborbital blade on the suborbital plate, although Carr dismissed these on the grounds that they also occur in more primitive arthrodires such as *Buchanosteus* and to some extent in forms like *Antineosteus*.

Carr (1991) recognized two main subgroups within the eubrachythoracids – coccosteomorphs and pachyosteomorphs. The coccosteomorph arthrodires are defined as monophyletic by sharing: (4) a preorbital plate embayment in the central plate; (5) reduction in medial contact between the preorbital plates; (6) spinous posterior margin on median dorsal plate; (7) posterior lateral plate with well-developed ventral lamina; (8) posterior ventrolateral plate with well-developed postpectoral lamina; (9) parasphenoid perforated by a foramen for the median hypophysial vein. Within the coccosteomorph group I recognize the following monophyletic groups: Incisoscutidae and Camuropiscidae (Denison 1984; Long 1988*b*, 1994; Carr 1991) and the Plourdosteidae (Vezina 1990; =Torosteidae Gardiner and Miles, 1990). The following synapomorphies define the clade containing the Plourdosteidae + Incisoscutidae + Camuropiscidae: (10) paranuchal sutures with postorbital plate, excluding contact between marginal and central plates; (11) anteroventral wings of the anterior lateral plate in contact with the interolateral plate (Long 1988*b*, Carr 1991). The Incisoscutidae and Camuropiscidae are united by the following synapomorphies (from Long 1988*b*,

1994): (12) spindle-shaped ('trullate') body form with elongate head shield; (13) cheek unit attached firmly to lateral margin of skull roof, precluding movement; (14) durophagous dentition; (15) parasphenoid having a rhombic, elongated shape. The plourdosteid group is defined by at least three other synapomorphies discussed in the text: (16) well-developed paired postocular processes; (17) the presence of an orbital autopalatine process on the suborbital bone; (18) a posterior lateral plate that forms part of the margin of the pectoral fenestra and is deeply inserted into the posterior dorsolateral plate. The deep insertion of the posterior lateral plate into the posterior dorsolateral plate was noted by Carr (1991) as a synapomorphy uniting *Eastmanosteus calliaspis* and the dinichthyids, in addition to four other synapomorphies, listed below. As the plourdosteid group is also well-defined by at least three synapomorphies (listed above) it is parsimonious to regard this feature as a parallelism between plourdosteids and the group *Eastmanosteus calliaspis* + dinichthyids.

The interrelationships of the pachyosteomorph, dinichthyid and aspinothoracid arthrodires have been discussed in depth by Carr (1991) and Lelievre (1991). Synapomorphies used by Carr to define these groups are as follows. Pachyosteomorphs share: (19) loss of the paranuchal embayment on the central plate; (20) reduction of contact between the nuchal and central plates; (21) formation of lateral contact between the suborbital and preorbital plates; (22) loss of the groove for the ventral portion of the main lateral line canal on the anterior dorsolateral plate.

Eastmanosteus calliaspis and the dinichthyids (as defined by Carr 1991) are united by the following synapomorphies: (23) position of the posterior margin of pineal plate posterior to orbits; (24) presence of a contact face for the posterior superognathal on the linguiform process of the suborbital plate; (25) presence of a groove for the main lateral line canal on the posterior dorsolateral plate; (26) presence of anterior and lateral cusps on the anterior superognathal. In Carr's analysis *Heintzichthys* and *Gorgonichthys* do not share any derived features with the dinichthyids, and in the light of new descriptions of *Heintzichthys* the analysis of dinichthyid interrelationships by Long (1987) is now redundant. *Heintzichthys* and *Gorgonichthys* share two derived features: (27) an anterior superognathal with an enclosed lateral face; and (28) the loss of adsymphysial denticles on the inferognathal bone.

The Aspinothoracidi (Stensiö 1959) are defined as a monophyletic group by the following synapomorphies from Carr (1991): (29) reduction of the lateral consolidated part of the head shield; (30) the anterior shift of the junction between the preorbital, central and postorbital plates to a new position over the orbit; (31) loss of the spinal plate; (32) closure of the angle between the postorbital and otic branches of the infraorbital canal, associated with the enlargement of the orbits. Finally, the selenosteids are defined by the presence of: (33) an enlarged orbit; and the following characters defined by Lelievre *et al.* (1987) – (34) denticulated gnathal plates; (35) loss of dorsal process on posterior superognathal plate; and (36) the development of an ethmoid crest.

This scheme leaves out many of the poorly known higher eubrachythoracids which require more complete material before their affinities can be resolved.

Interrelationships of plourdosteids. The taxonomic position of *Mcnamaraspis* as one of the plourdosteids can be demonstrated by the presence of characters (16)–(18) above. Gardiner and Miles (1990) united the Gogo plourdosteids with *Plourdosteus canadensis* on the strength of several general features in their family Torosteidae, but also noted the well-developed postocular processes as a synapomorphy of the group. Well-developed postocular processes are also known in some, but not all, dinichthyids (e.g. present in *Dunkleosteus terreli*; Heintz 1932; absent in *Eastmanosteus calliaspis* based on observation of Gogo specimens). In this respect they are regarded as a convergent feature in dinichthyids, a monophyletic group, if *Heintzichthys* and *Gorgonichthys* are excluded, as defined by Carr (1991).

Whether an orbital autopalatine process occurs on the suborbital plate of *Plourdosteus* is not yet known, although as similar specializations occur on the inner surface of the skull roof (such as the presence of a well-defined triangular depression mesial to the lateral consolidated area, the development of a hyoid process behind the postocular processes, based on observation of BMNH
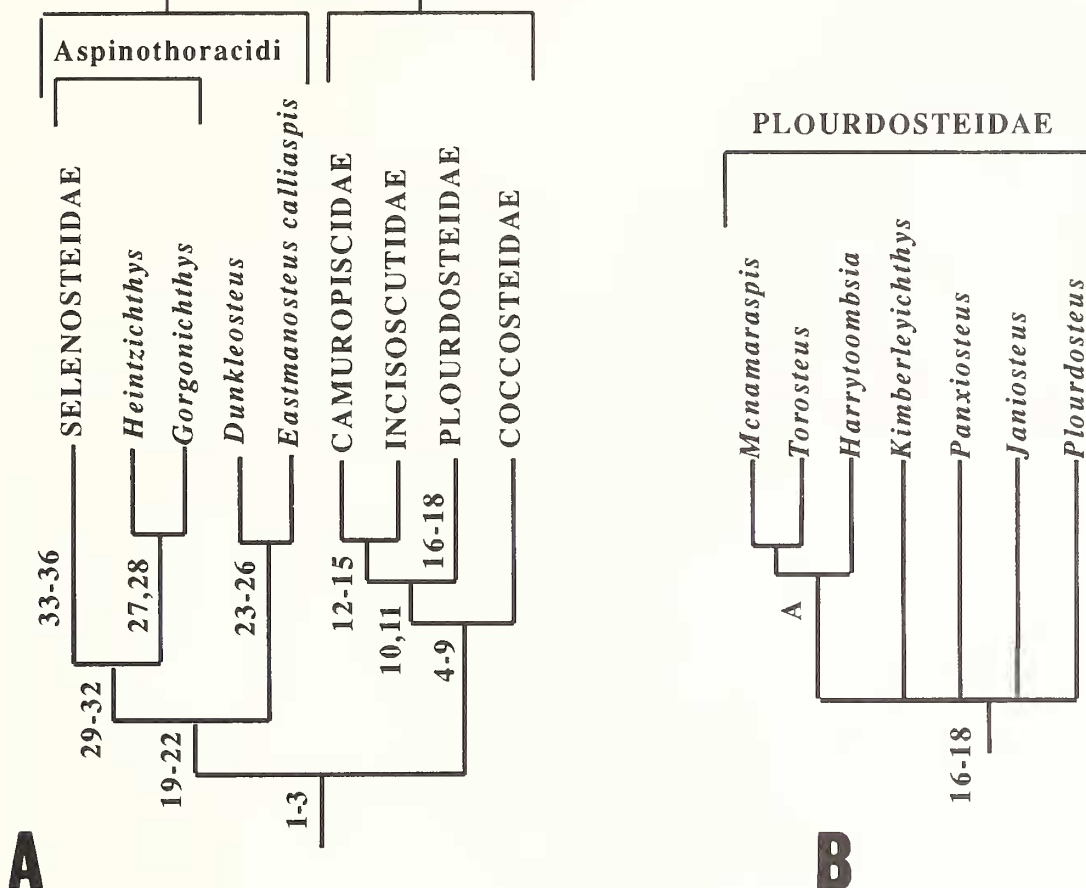
TEXT-FIG. 18. A, cladogram of higher eubrachythoracid interrelationships (after Carr 1991). B, cladogram of plourdosteid interrelationships. Synapomorphies are listed in text.

P60583), and the suborbital is of similar robust form, it is predicated that it should also be present in this genus.

Within the plourdosteid group several taxa share a number of derived features with polarity assessed by comparison with the coccosteid and dinichthyid outgroups. For example, the sizes of the marginal and postorbital plates are very similar in coccosteids and dinichthyids, and this is seen also in *Kimberleyichthys*, with increasingly larger postorbitals and smaller marginals in other plourdosteids. Thus the presence of very large postorbital plate relative to the size of the marginal plate may be an autapomorphy of *Panxiosteus*, but is of variable size range in other plourdosteids. The marginal plate is strongly indented into the postorbital plate in all plourdosteids except *Panxiosteus* and *Plourdosteus*, although this character is also of dubious phylogentic value as it is variable within coccosetids and dinichthyids. The large trilobate centrals of coccosteids and dinichthyids are also present in *Plourdosteus*, *Janiosteus*, *Panxiosteus* and *Kimberleyichthys*, but the posterior lobe is reduced in *Mcnamaraspis*, *Torosteus* and *Harrytoombsia*, here considered to be a synapomorphy (A) uniting these taxa. The parasphenoids are known in the Gogo forms and
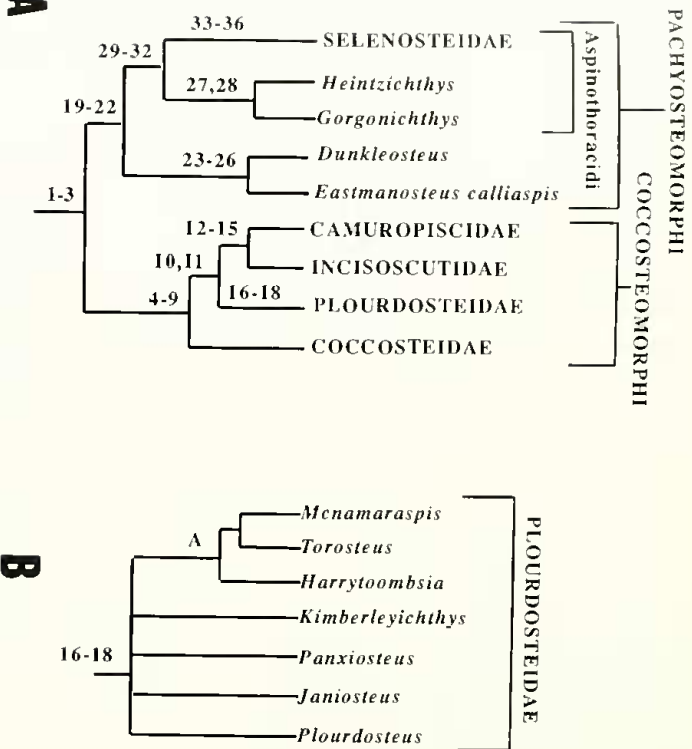
A

B

TEXT-FIG. 18. A, cladogram of higher eubrachythoraciid interrelationships (after Carr 1991). B, cladogram of plourdosteid interrelationships. Synapomorphies are listed in text.

P6053), and the suborbital is of similar robust form, it is predicted that it should also be present in this genus.

Within the plourdosteid group several taxa share a number of derived features with polarity assessed by comparison with the coccosteid and dinichthyid outgroups. For example, the sizes of the marginal and postorbital plates are very similar in coccosteids and dinichthyids, and this is seen also in *Kimberleyichthys*, with increasingly larger postorbitals and smaller marginals in other plourdosteids. Thus the presence of very large postorbital plate relative to the size of the marginal plate may be an autapomorphy of *Panxiosteus*, but is of variable size range in other plourdosteids. The marginal plate is strongly indented into the postorbital plate in all plourdosteids except *Panxiosteus* and *Plourdosteus*, although this character is also of dubious phylogenetic value as it is variable within coccosteids and dinichthyids. The large trilobate centrals of coccosteids and dinichthyids are also present in *Plourdosteus, Janiosteus, Panxiosteus* and *Kimberleyichthys*, but the posterior lobe is reduced in *Mcnamaraspis, Torosteus* and *Harrytoombsia*, here considered to be a synapomorphy (A) uniting these taxa. The parasphenoids are known in the Gogo forms and

Plourdosteus (Vezina 1990), but are not useful in refinement of plourdosteid relationships as they are of more or less uniform morphology.

The trunk shield is known in all the taxa save *Janiosteus* and only partially in *Pauxiosteus* and *Kimberleyichthys*. The most variable features are the shape of the posterior lateral plates and the extent of their external ornamentation. The loss of dermal ornamentation on these plates is seen in *Mcnamaraspis*, and to some degree in *Harrytoombsia* and *Torosteus pulchellus*, but the primitive condition of having extensive areas of dermal ornamentation is retained in *Kimberleyichthys*, *Torosteus tuberculatus* and *Plourdosteus*. In this respect, although the character is quite variable it lends support to the hypothesis that *Mcnamaraspis*, *Torosteus* and *Harrytoombsia* form an apomorphic subgroup within the Plourdosteidae. The extreme reduction of the spinal plate is an autapomorphy of *Mcnamaraspis* within the Plourdosteidae that is paralleled within the Coccosteidae in the similar development of a large pectoral fenestra and short spinal in *Watsonosteus*. Text-figure 18 summarizes the position of the plourdosteids within the higher eubrachythoracids, and shows an hypothesis of interrelationships of plourdosteids, based on the above discussion.

Placoderm relationships. The presence of annular cartilages in placoderms, based on the single specimen of *Mcnamaraspis*, demonstrates another similarity between placoderms and elasmo-branchs, as suggested by Stensiö (1963), although the exact form of the annular cartilages of *Mcnamaraspis* differs in many features from those of elasmobranchs. In elasmobranchs the annular cartilage is a complex folded cartilage of variable morphology that encircles both the incurrent and excurrent nares, whereas in *Mcnamaraspis* it is an ossified single unit with only one narial opening, and thus only borders the space for the excurrent naris.

Non-ossified cartilaginous annular cartilages were probably present in all arthrodires, based on the similar morphology of the cribrosal bones and shapes of the nasal regions (where preserved). The function of the annular cartilage, to divide the incurrent and excurrent nares from the common opening of the nasal capsule, and direct the flow of water around the olfactory organ, appears to be similar in both chondrichthyans and *Mcnamaraspis*. The convoluted folds of bone on the inner surface of the ossified annular cartilages shows clearly the direction of flow from the incurrent naris, around the outer surface of the olfactory organ, and out via the slit in one corner of the cartilage, this being interpreted as the excurrent naris. This character lends weight to the hypothesis of placoderms being more closely related to chondrichthyans (Stensiö 1963; Goujet 1984), rather than being a sister group to osteichthyans (Forey 1980; Gardiner 1984).

Young (1986) reviewed the evidence for placoderm relationships and argued that there was insufficient evidence for direct comparison of osteichthyan skull roof patterns with those of placoderms, and that other listed 'synapomophies' of placoderms and osteichthyans were often manifestations of a single character, such as the capacity to ossify the perichondrium. Young also preferred new interpretations of placoderm morphology and concluded that placoderms were either the sister group to all gnathostomes, or the sister group to chondrichthyans. The new observations that the arthrodires sometimes possessed an annular cartilage and that the suborbitalis division of the adductor mandibulae was probably developed as in chondrichthyans lend further support to the hypothesis that placoderms and chondrichthyans are sister groups.

Resolution of such higher taxonomic problems will seemingly rest on new discoveries of well-preserved placoderms from sites such as Gogo, where pertinent new anatomical information is coming to light with each season's fieldwork.

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JOHN A. LONG
Western Australian Museum
Francis St., Perth
Western Australia 6000